The Veliger 50(2):59–71 (June 20, 2008)

THE VELIGER
© CMS, Inc., 2007

Synecology of a Springsnail (Caenogastropoda: Hydrobiidae) Assemblage in a Western U.S. Thermal Spring Province

DONALD W. SADA

Division of Hydrologic Sciences, Desert Research Institute, 2215 Raggio Parkway, Reno, NV 89512, USA
(e-mail: Don.Sada@dri.edu), fax: 775/673-7363

Abstract. Springsnails are numerically dominant members of benthic communities in many springs of western North America and Australia. Several studies have shown the influence of water chemistry on their abundance and distribution within springs, but little information exists regarding their use of physical aspects of spring environments. Habitat preferences, niche breadth and overlap, and environmental factors influencing the structure of an assemblage of native springsnails (*Pyrgulopsis avernalis*, *P. carinifera*, and *Tryonia clathrata*) and the non-native red-rimmed melania (*Melanoides turberculata*) gastropod are described in a southern Nevada, USA, thermal spring province. Water temperature, current velocity, and substrate type were the most important physical factors structuring the assemblage. Springbrook wetted width, presence of armored and incised banks, and location of sample sites across the wetted width were also statistically significant, but less important factors. Each species occupied a wide diversity of habitats, but each species also exhibited habitat preferences for a range of depths, velocities, temperatures, or substrates. Niche overlap varied among species and habitats were partitioned among species for a minimum of two environmental resources. Competitive interactions appeared to minimally influence the structure and distributions of species belonging to this assemblage.

Findings suggest that springsnails are restricted to portions of a spring that provide suitable physicochemical conditions, and that each springsnail taxon may exhibit specific habitat requirements. Springsnail extinctions and declines in abundance in western North America and Australia can be attributed to human activities altering the discharge and water depth, substrate composition, current velocity, and water temperature of springs. Novel approaches are required to alter human uses and facilitate restoration, and protect the integrity of these unique arid land aquatic systems.

Key Words: Spring ecology, Hydrobiidae, springsnail ecology, arid land wetlands.

INTRODUCTION

The Hydrobiidae is a worldwide family of primarily freshwater gill-breathing gastropods. Recent taxonomic studies have found an amazing diversity of hydrobiids (commonly referred to as springsnails) in isolated, arid land springs of North America and Australia. More than 120 species in seven genera are known from more than 1000 springs in the western U.S., and 35 species in nine genera from Australia (Ponder et al., 1989; Hershler, 1994, 1998, 2001). Springsnails are restricted to persistent aquatic habitats that are minimally affected by drought (Taylor, 1985) and most species occupy few localized habitats within a limited geographic area (Hershler, 1998). They are usually the most abundant benthic macroinvertebrate in springs where they occur, and springs occupied by more than one springsnail species are uncommon.

In spite of their taxonomic diversity and their abundance in springs, few ecological studies have been conducted. Information is limited to demographic studies showing the influence of temperature on *Pyrgulopsis bruneauensis* demography and feeding in springs along the Snake River of southern Idaho (Mladenka and Minshall, 2001), and relationships between CO_2 concentrations and *P. montezumensis* abundance in northern Arizona (O'Brien and Blinn, 1999). Richards et al. (2001) examined spatial relationships in an assemblage of three snails including *Taylorconcha serpenticola* and Ponder et al. (1989) examined the influence of several environmental factors on activity and survivorship of several species in mound springs of Australia. These species responded to desiccation, salinity, deoxygenated water, water temperature, and submersion but the authors were unable to quantify relationships between habitat zones and springsnail abundance. Qualitative observations during taxonomic and biogeographic surveys suggested that abundance within a spring is influenced by water depth, current velocity, substrate composition, and aquatic vegetation (e.g., Hershler and Sada, 1987; Hershler, 1998). These observations indicate that each species occupies a unique habitat within a spring, but they have not been supported by quantitative studies examining relationships between spring environment, microhabitat use, and assemblage structure. Ecological information is needed to provide insight into isolating mechanisms that have facilitated development of this diverse fauna in small, isolated habitats. This information is also important in determining how springsnails respond to human activities that alter springs. These small wetlands support much of the aquatic life in arid lands and most springs have been degraded by livestock, diversion, and introduction of non-native species (Sada et al., 1992; Shepherd, 1993; Hubbs, 1995; Myers and Resh, 1999; Sada and Vinyard, 2002; Sada et al., 2005). These activities have justified listing several springsnail species as endangered in the western U.S., and Hershler (1998) and Sada (field notes) recorded three extinctions and extirpation of 13 populations in the past decade.

In this study, an assemblage of four species (three springsnails and one non-native mollusk) was examined in a thermal spring province to: 1—determine physical factors (in addition to temperature) affecting assemblage structure, 2—quantify microhabitat use, and 3—determine if habitat use differs among species. The spring province includes approximately 30 springs that discharge a total of 1.3 m^3/sec. Discharge and temperature at individual springs ranges from 10–200 l/min, and 24.5–31.8°C, respectively. This assemblage included *Pyrgulopsis avernalis* and *P. carinifea* that are endemic to this province, and *Tryonia clathrata* that is endemic to thermal springs along the pluvial White River system in eastern Nevada (Hershler, 1994, 2001). All of these species are small. The shell height of *P. avernalis* ranges from 2.4 mm to 4.3 mm, for *P. carinifera* from 3.8 mm to 5.0 mm, and for *T. clathrata* from 2.9 mm to 7.0 mm. The red-rimmed melania (*Melanoides tuberculata*, family Thiaridae), which is native to Asia (Burch and Tottenham, 1980), also inhabits these springs. Shell height of adult melania is from 1 cm to 3 cm. Quantitative studies have not assessed the influence of this species on springsnails. Hershler and Sada (1987) noted that springsnail abundance may be decreased in its presence, and Pointier et al. (1993) and De Marco (1999) found that it detrimentally affected native gastropod abundance.

This work was one component of studies examining the benthic macroinvertebrate communities in this spring province, which will be the subject of a subsequent article.

SITE DESCRIPTION

Studies were conducted in a spring province (collectively referred to as 'Warm Springs') that forms the Muddy River in Clark County, Nevada (Figure 1). The Muddy River flows approximately 35 km into the Colorado River (which is now within the Overton Arm of Lake Mead). The springs creating the Muddy River are located at approximately 500 m elevation and scattered over approximately 2,000 hectares. Water flows through approximately 4 km of springbrook before forming the Muddy River. Water temperature at spring sources is approximately 32°C, and combined discharge from the province is a relatively constant 1.5 m^3/sec (Eakin, 1964). Discharge from individual springs ranges from approximately 0.0028 to 0.17 m^3/sec and spring brooks are bordered by ash (*Fraxinus velutina*), mesquite (*Prosopis* sp.), non-native salt cedar (*Tamarisk* sp.), and fan palm (*Washingtonia filifera*). These woody species are interspersed with grasses (mostly *Distichlis spicata*) and perennial herbs. Springbrooks support diverse aquatic habitats from low gradient brooks that meander over fine substrates to higher gradient brooks where swift water flows over gravel and cobble substrates. General characteristics of spring brooks that were sampled during this study are summarized in Tables 1 and 2. In addition to mollusks, these springs support a number of rare fishes and other aquatic macroinvertebrates, many of which are endemic to Warm Springs (U.S. Fish and Wildlife Service, 1996, Hershler, 1994, 2001; Schmude, 1999; Polhemus and Polhemus, 2002; Sada and Vinyard, 2002).

Native Americans had settlements near Warm Springs, and in the early 19th Century it was settled by white men. Its springs have been altered for recreation and diversion, channelization, and siltation from agriculture, and non-native fishes and aquatic invertebrates have been introduced (Scoppettone, 1993). These alterations reduced native fish abundance and resulted in listing the Moapa dace (*Moapa coriacea*) as endangered by the U.S. Fish and Wildlife Service (U.S. Fish and Wildlife Service, 1996). Since the early 1980s, Moapa dace recovery programs have restored six springs and approximately 600 m of spring brook (approximately 15 percent) to natural condition.

METHODS

Data Collection

Aquatic habitat parameters (Tables 1 and 2) and mollusks were sampled in 84, 10 cm × 12 cm quadrats at 21 stations located at predetermined distances from five spring sources (two with long and three with short spring brooks) (Table 3) during the autumn of 1996. Sample stations included the diversity of habitats in first-order spring brooks, and were placed near springs sources and along the downstream continuum to the confluence of the nearest tributary spring brook. The distance of stations from spring sources varied because

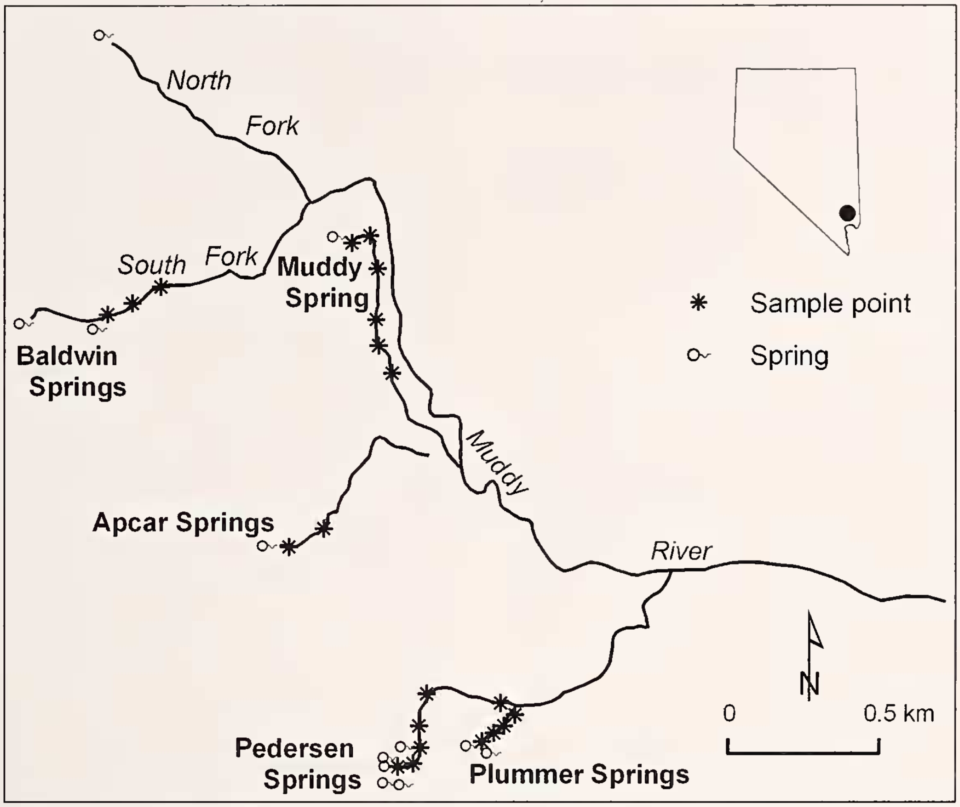

Figure 1. Map showing the approximate location of sample sites (*) and major springs in the 'Warm Springs' province that combine to form the Muddy River, Clark County, Nevada.

some reaches were not easily accessed, some spring brooks were less than 50 m long, and longer intervals occurred in large springs with long spring brooks. Each station consisted of four transects spanning the wetted width (spaced 1 m apart and oriented perpendicular to the thalweg) where mollusk samples and aquatic habitat measurements were collected from two mid-channel and two springbrook margin quadrats. Mid-channel quadrats were placed along first and third

Table 1

Median and range of aquatic habitat parameters measured (units shown in parentheses) within quadrats and at 21 stations where mollusks were sampled in Warm Springs, upper Muddy River. All variables used in CCA to examine relationship between environmental factors and mollusk assemblage structure. * = parameters measured in quadrats, ** = parameters measured along transects, all others measured at stations.

Element	Median	Range
Water Depth (cm)*	16	2–70
Water Velocity (cm/sec)*	20	0–109
Springbrook Width (cm)**	180	40–530
Water Temperature (°C)	31.3	24.5–31.8
Dissolved Oxygen (mg/l)	5.1	4.1–5.7
Electrical Conductance (µmhos/cm)	1100	1050–1100
pH	7.6	7.4–7.6
Riparian Cover (percent)**	90	2–100

Table 2

Proportion of quadrats and spring brook banks where substrate and channel features, respectively, occurred during mollusk sampling in Warm Springs, upper Muddy River, Clark County, Nevada. n = 84 for Substrate Features (all measured in quadrats) and n = 168 for Channel Features (all measured where transects intersected banks). All variables used in CCA.

Substrate Feature	Proportion	Channel Feature	Proportion
Fines	0.28	Stable Channel	0.87
Sand	0.18	Incised Banks	0.75
Gravel	0.44	Bank Overhang	0.57
Cobble	0.11	Bank Perennial Vegetation	0.42
CPOM	0.16	Grassy Banks	0.14
Palm Roots	0.43	Armored Banks	0.14

Table 3

Spring brook names and the approximate distance of sample stations from each spring source.

Springbrook Name	Locations (m)
Pedersen Spring	10, 25, 60, 120, 200, 500
Muddy Spring	10, 25, 60, 120, 180, 280
Plummer Spring	10, 25, 60, 120
Apcar Spring	25, 60
South Fork Muddy River Spring	25, 60, 120

transects, and right and left bank quadrats on transects two and four, respectively (bank quadrats scored 1 and mid-channel scored 0 for canonical correspondence analysis). Channel features (Table 2) and springbrook width were recorded across each transect and bank features were recorded where transects intersected the banks. Water depth and mean water column velocity (measurement taken at 60 percent water depth) were measured at the center of each quadrat, and occurrence of substrate types, filamentous green algae, palm roots, and coarse particulate organic matter (CPOM) were scored as present (1) or absent (0) from a quadrat. Electrical conductance (EC), dissolved oxygen concentration, temperature, and pH were measured at each station (using Model 33 [EC and temperature] and Model 57 YSI [dissolved oxygen] meters, and an Oakton pHTestr 2 handheld meter). A Marsh-McBirney Model 2000 current meter was used to measure current velocity. Although this velocity measurement may weakly quantify benthic microhabitats, correlation between these velocities suggests that conditions at mean water column are indicative of velocities over substrate. pH and dissolved oxygen meters were calibrated daily and other meters calibrated according to manufacturer specifications. Mollusks were collected by roiling substrate within the quadrat for 10 sec to flush material downstream into a 250 micron mesh net that was held in a vertical frame and secured to the quadrat. Samples were preserved in 90 percent ethyl alcohol and returned to the laboratory for identification, and enumeration. Identification was made using descriptions in Hershler (1994, 2001). Samples are archived at the Desert Research Institute, Aquatic Ecology Laboratory, Reno, Nevada.

Data Analysis

Environment-Assemblage Relationships: Relationships between aquatic and channel environments and assemblage structure were examined with canonical correspondence analysis (CCA) using Canoco 4.0 for Windows. CCA axis scores were standardized using methods of Hill (1979), scaled to optimize the representation of species, and Monte Carlo simulation (1000 iterations) tested the hypothesis that there was no relationship between species and environment matrices. A total of 22 measured and categorical habitat features were included in the analysis (EC and pH did not differ among stations and were not used in the CCA). The CCA is a multivariate direct gradient analysis that analyzes unimodal data to assess species distribution along environmental gradients. It performs multiple linear least-squares regressions with the environment and species abundance as independent and dependent variables, respectively (ter Braak and Prentice, 1988; Jongman et al., 1987; Palmer, 1993).

Microhabitat Use: Habitat preference was calculated for water depth, temperature, and velocity, and the presence of substrate types. With the exception of water depth, CCA showed these variables were most important to structuring the molluscan assemblage (Figure 2, Table 4). Preferences for water depth were calculated because preliminary analysis indicated these species occupied a diversity of available depths. Preference was calculated using the formula of Jacobs (1974): $D = r - p/ r + p - 2rp$; where p is the proportion of the resource available in the habitat and r is the proportion of the resource utilized by the species. Resource use was categorized as moderate preference (between 0.25 and 0.5) or strong preference (>0.5), or strongly (<-0.5) or weakly avoided (between -0.25 and -0.5). Neither preference nor avoidance were indicated by values $<$ 0.24 and > -0.24. Niche breadth was calculated using the equation $B = 1/\sum P_{ij}^2$, where P_{ij} is the proportion of the resource in each category (Levins, 1968), and niche overlap was calculated using the same variables following the equation from Schoener (1970) with revisions by Litton et al. (1981) so that $S = 100(1-1/2 \sum|P_{xi} - P_{yi}|)$ where P_{xi} and P_{yi} are the proportion of resource use in each category for the two species being compared. Niche breadth values may range from 1 − > 14. Low values are indicative of narrow, limited habitat use and high values indicate wider use of available habitats. Niche overlap values range from 0 to 1 with substantial overlap being indicated by values $>$ 0.5 and differences in use indicated by values $<$ 0.5. Habitat availability was calculated using records from all quadrats ($n = 84$) and habitat use, and niche breadth and overlap calculations were made by weighting resource utilization in accordance with each species' abundance. Preference, niche breadth, and niche overlap calculations must be interpreted with caution. They are indices that provide insight into relationships in habitat use among species but they are not quantitative descriptions of inter-specific interactions, which can only be determined through experimental manipulation. Similarities among results of these analyses and CCA may guide experimental studies by indicating the relative influence of individual environmental variables on the distribution of species.

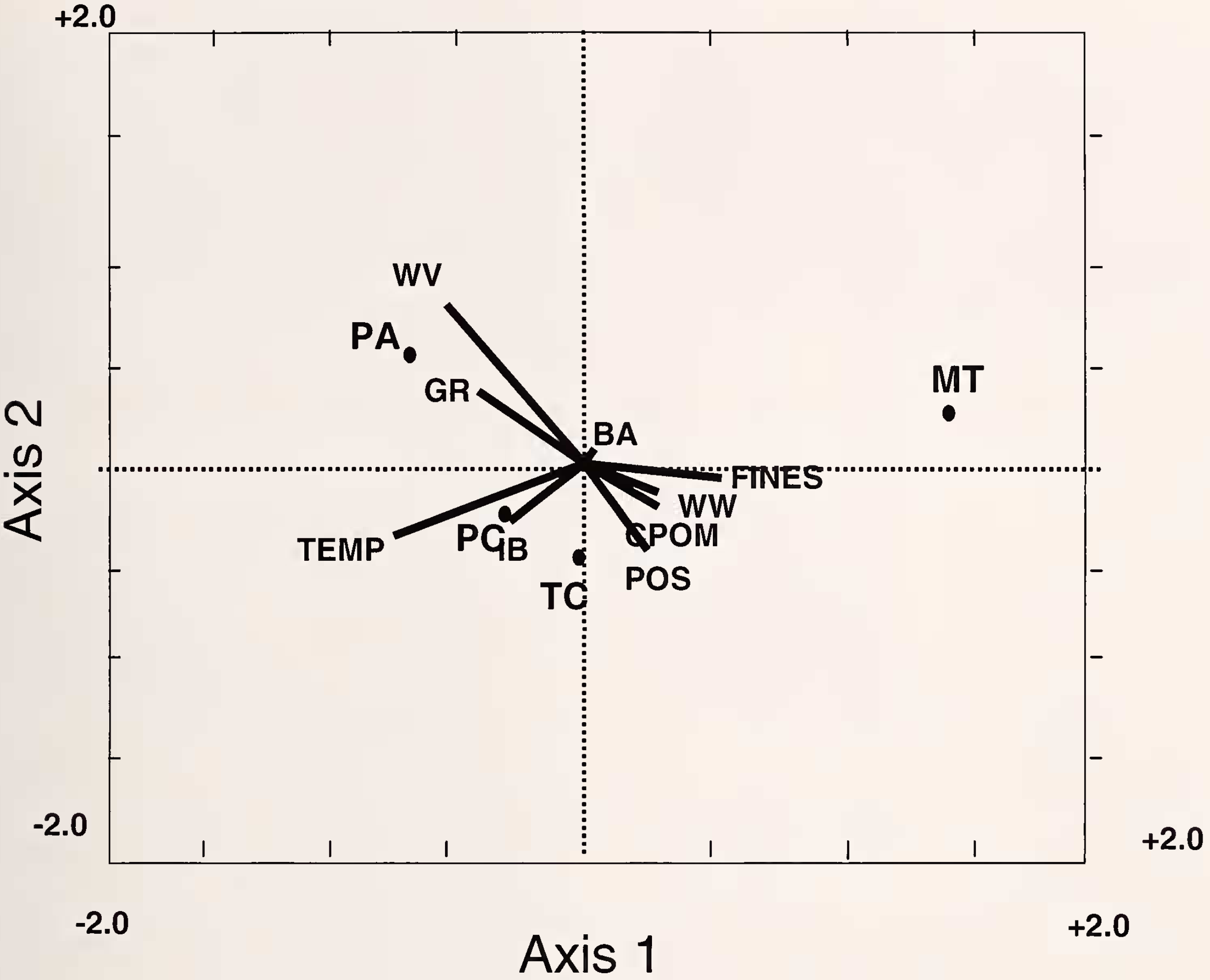

Figure 2. Canonical correspondence analysis biplot showing the relative influence of significant instream and channel environmental parameters on structure of the mollusk assemblage at Warm Springs. The relative influence of each environmental variable is shown by vector length with longer vectors indicating variables with greater importance. PA = *P. avernalis*, PC = *P. carinifera*, TC = *T. clathrata*, MT = *M. tuberculata*, WV = mean water column velocity, TEMP = water temperature, GR = gravel, FINES = fines, IB = presence of incised banks, POS = quadrat position, CPOM = coarse particulate organic matter, WW = wetted (spring brook) width, and BA = presence of armored bank.

RESULTS

Environment-Assemblage Relationships: A total of 1282 *P. carinifera*, 704 *P. avernalis*, 750 *T. clathrata*, and 283 *M. tuberculata* were collected and tallied. Snail abundance in quadrats ranged from 0 to 346 (equivalent to approximately 29,000/m^2), and from 0 to 148 for *P. carinifera*, 0 to 145 for *P. avernalis*, 0 to 96 for *T. clathrata*, and 0 to 34 for *M. tuberculata*. Initial CCA revealed nine significant ($P < 0.05$) physicochemical factors were most important to structuring the assemblage (Table 4). Water temperature, mean water column velocity, the presence of some substrates (fines, gravel, CPOM), aspects of channel morphology (incised or armored banks, spring brook width), and quadrat location (bank vs. mid-channel) were statistically significant variables. Water depth, the presence of roots, algae, other submerged vegetation, sand and cobble substrates, dissolved oxygen concentration, distance from spring source, and bank angle, stability and grassy vegetation had comparatively little influence on assemblage structure. The first axis explained most of the species-environment relationship, all variation was explained by the first three canonical axes, and the total intertia of eigenvalues was 0.814 (Table 5). Monte Carlo simulation (1000 iterations) of species-environment correlations were significant for Axis 1 (P = 0.001) and for all canonical axes (P = 0.001).

Figure 2 is a CCA biplot where species relationships and environmental factors that were most influential to

Table 4

Inter-set correlations for 22 environmental variables examined during CCA. Variables in bold were statistically significant ($P < 0.05$) and used in final analysis for the biplot in Figure 2. Abbreviations used in Figure 2 shown in parentheses.

Environmental Variable	Axis 1	Axis 2	Axis 3
Water Depth	−0.094	−0.0036	0.0704
Water Velocity (WV)	−0.5619	−0.0036	0.0704
Wetted (Spring Brook) Width (WW)	0.302	−0.0772	0.2246
Presence of Palm Roots	−0.033	−.01297	−0.0597
Presence of Fines (FINES)	0.5465	0.0196	0.0459
Presence of Sand	−0.1301	0.042	−0.1521
Presence of Gravel (GR)	−0.3831	0.128	−0.041
Presence of Cobble	−0.071	−0.0007	0.1061
CPOM (CPOM)	0.2866	−0.1245	−0.0369
Dissolved Oxygen Concentration	0.0511	.0855	−0.3521
PH	0.1421	−0.1228	0.1427
Water Temperature (TEMP)	−0.6796	−0.3401	0.0182
Electrical Conductance	−0.0643	−0.1221	0.1527
Bank Angle	0.0965	0.0296	0.1444
Presence of Bank Overhang	−0.1707	0.2148	−0.032
Bank Armor Presence (BA)	0.0965	0.0296	0.1444
Grassy Bank Presence	0.0582	−0.2636	0.188
Presence of Other Perennial Vegetation on Bank	0.0596	−0.234	−0.0447
Incised Bank Presence (IB)	−0.2142	−0.1887	0.0907
Stable Banks	−0.1032	−0.2497	−0.1421
Riparian Cover	−0.0439	0.0816	0.0804
Quadrat Position (Bank or Center) (POS)	0.2823	−0.2859	−0.0651

assemblage structure are illustrated by vector length and the association of each species with each environmental variable. Vector length illustrates that water velocity, temperature, and the presence of fines and gravel were the most influential factors. Quadrat position and the presence of incised banks were moderately influential, and wetted width, and the presence of CPOM and armored banks were least important. The plot indicates these species occupied different habitats. *Pyrgulopsis avernalis* (PA) was associated with higher current velocities (WV), gravel substrate (GR), and higher water temperature (TEMP), and *P. carinifera* (PC) with moderate current velocities and incised (IB), unarmored banks. *Tryonia clathrata* (TC) was associated with moderate temperatures, slower currents, bank quadrats, CPOM, and the absence of gravel and fine substrates. *Melanoides tuberculata* was associated with fine substrate (FINES), wider brooks (WW), cooler temperatures, and lower current velocities.

Table 5

Eigenvalues, species-environment correlations, and cumulative percentage variance of species data and species-environment relationship explained by the first three ordination axes of the CCA analysis of the Warm Springs mollusk assemblage.

	Axis I	Axis II	Axis III	Total Inertia
Eigenvalues	0.361	0.123	0.023	0.841
Species-Environment Correlation	0.835	0.748	0.471	
Cumulative Percentage Variance				
Species Data	42.9	57.5	60.3	
Species-Environment Relation	71.2	95.5	100	

Microhabitat Use and Resource Partitioning: Habitat preference calculations confirm CCA results and indicate these species partition habitat by temperature, water velocity, and substrate. Niche breadth and overlap values suggested that there were differences in diversity of habitat used by each species and that there was common use of some habitats. *Pyrgulopsis avernalis* occupied a wide diversity of depths (B = 5.21), but preferred depths from 30 cm to 40 cm (Figure 3A). It avoided shallow (<15 cm) and deeper water (>45 cm). Niche breadth values indicated that it also occupied a wide variety of current velocities (B = 7.69), but it preferred mean water column velocities > 50 cm/sec and strongly preferred velocities approximately 70–110 cm/sec (Figure 4A). It avoided currents < 40 cm/sec and it was most common in mid-channel quadrats where currents were swift and smaller substrates scarce (Table 6). It also preferred gravel, avoided cobbles, and strongly avoided fines, sand, and CPOM (Figure 5A). It occupied the warmest water temperatures in the spring province, preferred temperatures near 32°C (B = 1.49), and avoided cooler water (Figure 6A).

Pyrgulopsis carinifera also occupied a diversity of depths (B = 5.29), but it preferred habitats < 10 cm deep and avoided depths > 30 cm (Figure 3B). It occupied slow and fast currents (B = 5.66) but preferred mean water column velocities from 30 to 40 cm/sec (Figure 4B). Like *P. avernalis*, it occurred in mid-channel quadrats (Table 6), preferred gravel, avoided sand and CPOM, and strongly avoided fines and cobbles (Figure 5B). It also strongly preferred temperatures near 32°C (B = 1.31) and avoided cooler water (Figure 6B).

Tryonia clathrata also preferred the warmest waters (Figure 6C), but occupied substantially different microhabitats than either species of *Pyrgulopsis. Tryonia clathrata* was most common along spring brook banks where it preferred shallow (<5 cm deep), slow moving

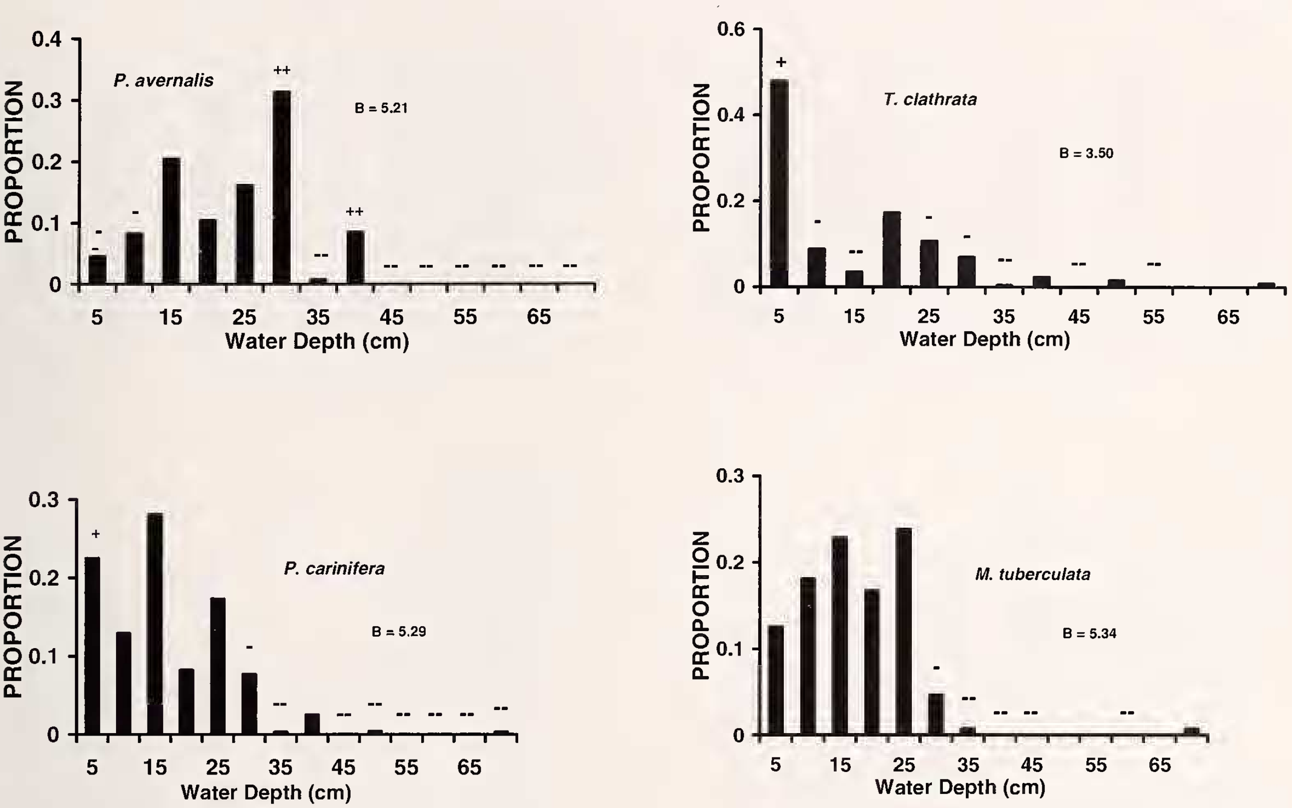

Figure 3. The depth of water occupied by *P. avernalis*, *P. carinifera*, *T. clathrata*, and *M. tuberculata*. + and ++ = moderately preferred resource categories, respectively, - and -- = moderately and strongly avoided resource categories, respectively. B = niche breadth.

(<20 cm/sec) water while avoiding deeper, swiftly flowing waters (Figures 3C and 4C, Table 6). Small niche breadth values for depth and velocity (B = 3.50 and 2.82, respectively) indicate its comparatively restricted use of shallow depths and slow currents. It strongly preferred sand, preferred fines and CPOM, and strongly avoided gravel and cobbles (Figure 5C).

Melanoides tuberculata occupied a wider diversity of water temperatures than the springsnails (B = 2.85), and it strongly preferred temperatures near 25°C and strongly avoided the warm temperatures preferred by springsnails (Figure 6D). Differences between springsnail and *M. tuberculata* preferences for temperature probably account for the importance of temperature in structuring the assemblage that was shown by CCA (Figure 2). It exhibited no preference for water depth but it strongly avoided habitats deeper than 30 cm (Figure 3C). It was most common along springbrook banks (Table 6). Current velocities from 0–10 cm/sec were preferred and mean water column velocities < 10 cm/sec were strongly preferred (Figure 4D). It showed no preference or avoidance of CPOM.

Melanoides tuberculata used habitats similar to those occupied by *T. clathrata* and quite different from both *Pyrgulopsis* species. Although habitats used by *T. clathrata* and *M. tuberculata* were similar, *M. tuberculata* strongly preferred the presence of fine substrate and strongly avoided sand, gravel, and cobble (Figure 5D). These two species also appeared to occupy habitats with different temperatures and current velocities (Figures 3D and 4D, respectively). *Tryonia clathrata* occupied shallow habitats (Figure 2D) where sand substrate was associated with slightly swifter current while *M. tuberculata* occupied habitats where fine substrates were associated with very low current velocities. These characteristics suggest that *M. tuberculata* may be relatively tolerant of nocturnal decreases in dissolved oxygen concentrations that can be associated with fine substrates. Use of this habitat type is consistent with observations of its habitat use by Dudgeon (1989), Gutiérrez et al. (1997), and Duggan (2002). Differences in habitat use by springsnails and *M. tuberculata* suggest that their interactions may be minimal at Warm Springs.

Niche overlap values generally confirm habitat use shown in Figures 3–5. Values were < 0.5 between *T. clathrata* and both species of *Pyrgulopsis* for water depth and substrate type (with exception of 0.638 between *T. clathrata* and *P. carinifera* for depth), which suggests that intra-generic habitat use of species in this

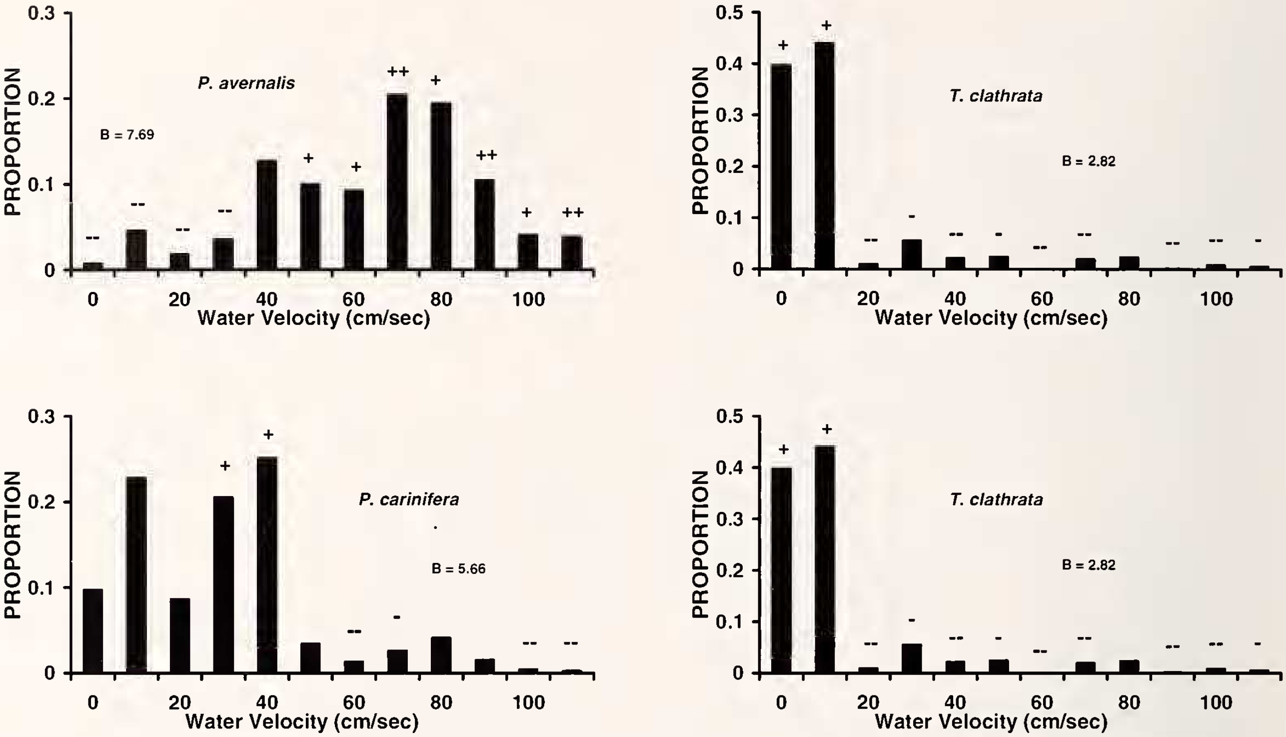

Figure 4. Mean water column velocity of habitats occupied *P. avernalis*, *P. carinifera*, *T. clathrata*, and *M. tuberculata*. Preference and avoidance illustrated as in Figure 3.

springsnail assemblage is minimal (Tables 7 and 8). Niche overlap values for *P. avernalis* and *P. clathrata* were low for current velocity (<0.35) and > 0.5 for water depth and substrate type, which indicates that habitat use by these species is similar and differs primarily in the use of fast and moderate currents by *P. avernalis* and *P. clathrata*, respectively. Overlap between the springsnail assemblage and *M. tuberculata* was high for water depth, but overlap was also high between velocities used by the melania, *P. carinifera*, and *T. clathrata* (Table 7). Highest overlap in current velocity occurred between *T. clathrata* and *M. tuberculata*, and lowest was between *P. avernalis* and *M. tuberculata* (Table 7). Overlap for fines, gravel, and cobble substrate use was relatively high among all species in the assemblage, but overlap was low between both *Pyrgulopsis* species and *T. clathrata* for use of sand (Table 8). Overlap for use of sand was also low between *M. tuberculata* and *T. clathrata* (Table 8), which confirms results of calculations showing *M. tuberculata* and *T. clathrata* preferred fines and sand, respectively.

DISCUSSION

Springsnails represent the most diverse family of gastropods in western North America and many species occupy the smallest aquatic habitats in the most arid regions of the continent. In these areas, most populations inhabit isolated springs and spring provinces on valley floors and along the base of mountain blocks. Populations rarely inhabit springs higher than 2,400 m elevation. Temperature and EC of springsnail habitats range from 10°C to 40°C and from 70 µmhos/cm to 37,000 µmhos/cm, respectively (Hershler and Sada, 1987; Sada and Deacon, 1995; Hershler, 1998). The amount of habitat occupied by springsnail populations ranges from < 1 m^2 in small springs to > 100 m^2 in large springs. Hershler (1998) estimated that the density of some populations may reach 10,000/m^2. Most populations are relictual in aquatic systems that have persisted since ancient pluvial periods, and they are restricted to springs with minimal environmental

Table 6

Proportion of individuals of each species of mollusk occurring in spring brook mid-channel and bank quadrats sampled at Warm Springs.

Species	Mid-Cannel	Bank
P. avernalis	0.80	0.20
P. carinifera	0.53	0.47
T. clathrata	0.18	0.82
M. tuberculata	0.24	0.76

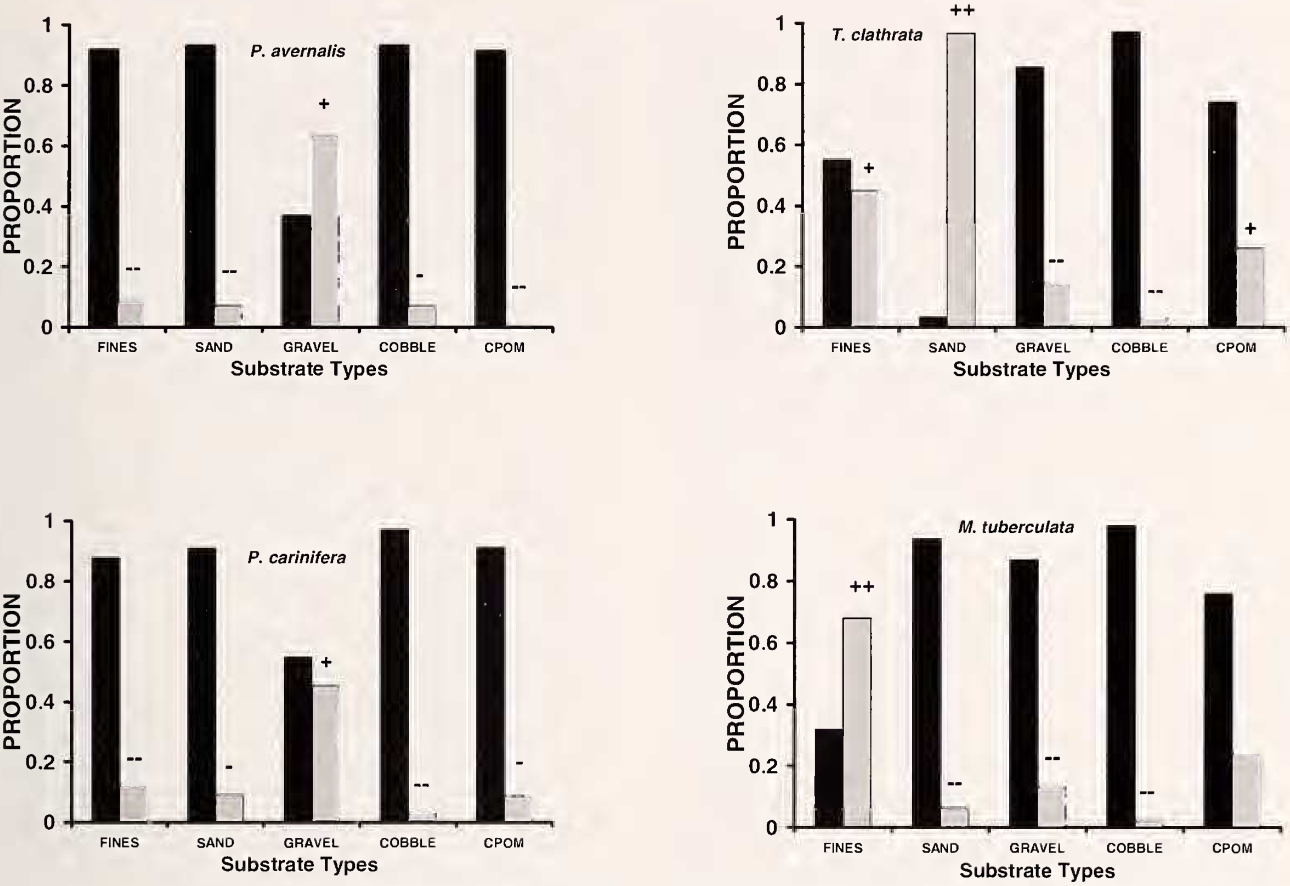

Figure 5. The proportion of *P. avernalis*, *P. carinifera*, *T. clathrata*, and *M. tuberculata* that were associated with the presence (☐) and absence (■) of different substrates. Preference and avoidance shown only for occupation of quadrats with the presence of a substrate type listed. Preference and avoidance illustrated as in Figure 3.

variability (Taylor, 1985). As with other crenobiontic species, densities are greatest near spring sources where physicochemical environments are relatively stable compared to downstream reaches of spring brooks where seasonal and daily environmental variability is relatively high and springsnails are sparse or absent (Noel, 1954; Hershler, 1998; McCabe, 1998). They do not inhabit reaches that dry on a regular basis, but they may colonize downstream reaches where stressful events such as flooding and drying are infrequent.

Past quantitative studies suggest that springsnails preferentially occupy limited portions of springs with suitable chemistry. In laboratory experiments O'Brien and Blinn (1999) demonstrated that *P. montezumensis* inhabited a limited reach of spring brook where CO_2 concentrations ranged from 110–315 mg/L. They did not occupy upstream reaches where concentrations were greater and downstream reaches where concentrations were less. Annual patterns of variability in *P. bruneauensis* density and its preference for upstream portions of spring brook were attributed to water temperature by Mladenka and Minshall (2001). In experiments with springsnail assemblages in mound springs of Australia, Ponder et al. (1989) demonstrated the influence of several environmental factors on activity levels and survivorship of one amphibious species and several aquatic species. Each of these species exhibited intolerance to desiccation, low and elevated salinity concentrations, deoxygenated water, low and elevated water temperature, and to varying exposure to submersion. Behavioral responses to light also varied among species. These studies also recorded the relative abundance of several species in eight zones (e.g., spring source, upper part of outflow, middle part of outflow, etc.) in a number of springs. Patterns of zonal occupation were weak, but each assemblage typically included one amphibious species and one large species, and from one to three small aquatic species. They also concluded that springsnail niche potential was fully exploited in these springs and that introduction of species from other springs was therefore unlikely.

The study at Warm Springs showed that structure of this assemblage of native and non-native mollusks was influenced by water temperature and several physical

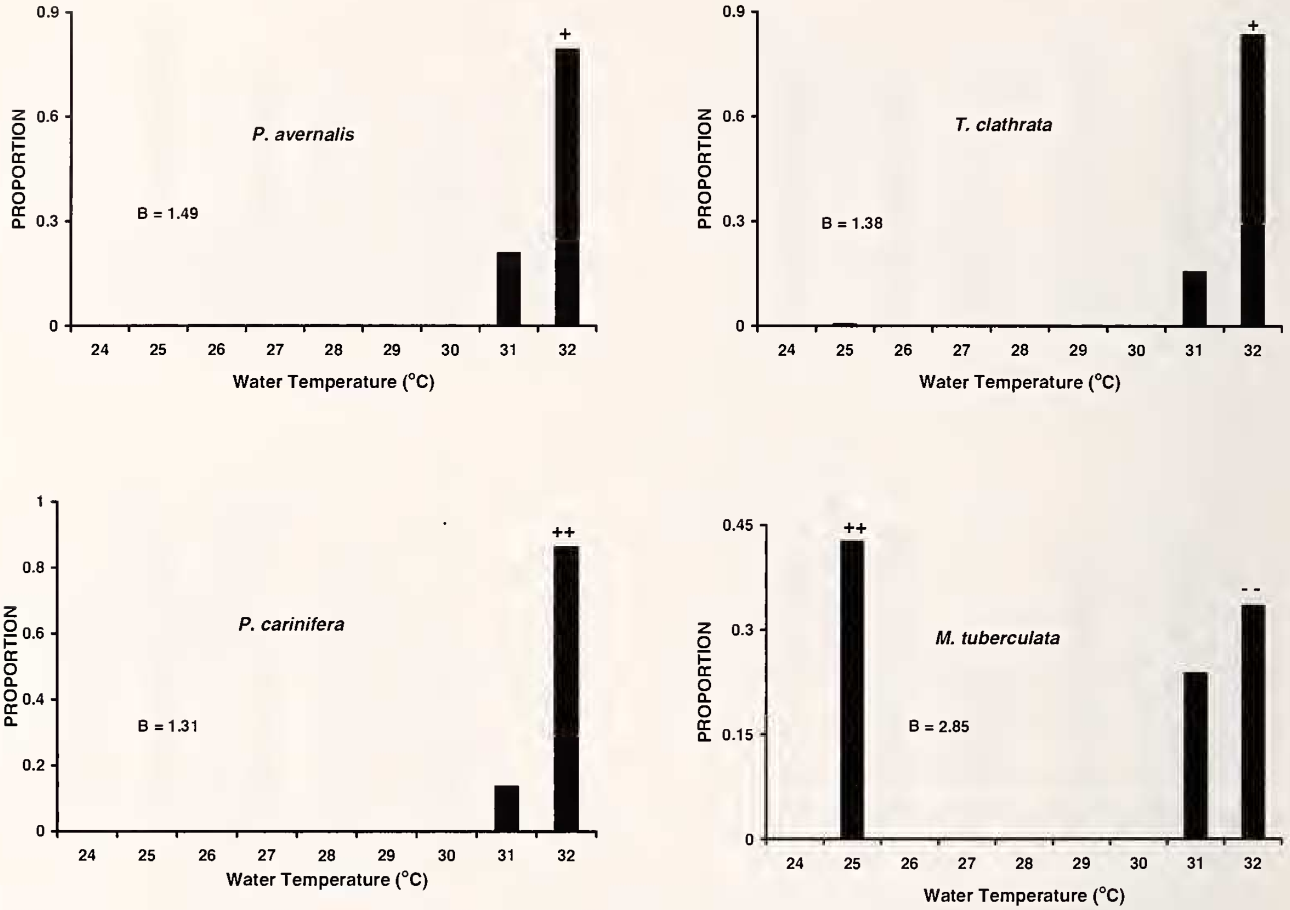

Figure 6. Water temperature of habitats occupied by *P. avernalis*, *P. carinifera*, *T. clathrata*, and *M. tuberculata*. Preference and avoidance illustrated as in Figure 3.

elements of the aquatic and spring brook bank environment. These conclusions appear to confirm qualitative observations made during taxonomic studies. They are also consistent with observations by Mladenka and Minshall (2001) that water temperature was an important element of their occupied habitat. Although springsnails at Warm Springs preferred warm water, preferences for temperature did not differ among these species and temperature was not an important factor segregating springsnail habitat use.

Springsnails at Warm Springs occupied a wide diversity of aquatic habitats, which was indicated by relatively high niche breadth values for each species in several habitat elements. Depths, velocities, and substrates occupied by *T. clathrata* were generally more specific than those occupied by either species of *Pyrgulopsis*. Both *Pyrgulopsis* generally occupied deeper and swifter water, and larger substrates than *T. clathrata*, which preferred water < 5 cm deep, velocities < 20 cm/sec, and sand and fine substrates.

Additional partitioning among assemblage members is suggested by the use of mid-channel and springbrook margin habitats. Although each species occurred across springbrooks, most *T. clathrata* occurred along spring brook margins, *P. carinifera* was relatively evenly distributed between margins and the mid-channel, and *P. avernalis* was most abundant in mid-channel habitats. This appears to be consistent with habitat

Table 7

Niche overlap values for water depth and mean water column velocity among mollusks in Warm Springs, Clark County, Nevada. Abbreviations for species as shown in Figure 2.

	Water Depth			
	PA	PC	TC	MT
PA		.678	.469	.649
PC	.366		.638	.789
TC	.197	.482		.579
MT	.159	.502	.877	
	Mean Water Column Velocity			

Table 8

Niche overlap values for fines, sand, gravel, and cobble substrates among mollusks in Warm Springs, Clark County, Nevada. Abbreviations for species as shown in Figure 2.

	Fines/Sand			
	PA	PC	TC	MT
PA		.961/.979	.635/.103	.404/.994
PC	.818/1		.674/.124	.443/.973
TC	.510/1	.692/1		.769/.097
MT	.500/.991	.500/.991	.500/.991	
	Gravel/Cobble			

preferences exhibited by each species. *Tryonia clathrata* occupied shallow, slow habitats and fine substrates that occured along springbrook banks. *Pyrgulopsis avernalis* was most abundant in mid-channel habitats where substrates are larger and depths and current velocities greatest and *Pyrgulopsis carinifera* preferred slower water and moderate depths that are lateral habitats in mid-channel and along springbrook margins. Preferential occupation of margin and mid-channel habitats suggests that these springsnails may exhibit zonal preferences of habitat use. Differences between this observation and conclusions by Ponder et al. (1989) that zonal preferences were not apparent may be attributed to sample techniques. The wide range in springsnail density within 120 cm^2 quadrats (range from 0 to 346 springsnails) at Warm Springs suggests there is wide spatial variability in springsnail abundance in a spring and that sample methods using large quadrats may yield weak relationships between springsnail abundance and characteristics of the spring environment. Determining these relationships appears to require quantitative sampling within a small area. Sampling springsnail abundance and habitat characteristics within 120 cm^2 quadrats appears suitable to examination these relationships.

Observations at Warm Springs provide insight into the potential effects of the *M. tuberculata* on springsnail populations. Observations of potential competitive interactions between *M. tuberculata* and several species of *Tryonia* and *Pyrgulopsis* in Ash Meadows, another thermal spring province in southern Nevada, that were hypothesized by Hershler and Sada (1987) were not confirmed at Warm Springs. Niche overlap between *M. tuberculata* and both species of Warm Springs *Pyrgulopsis* was small for all measured habitat elements. Overlap between *M. tuberculata* and *T. clathrata* was more extensive with both species occupying marginal, slow moving habitats with small substrate. In spite of these similarities, interactions appeared to be minor because they utilized different temperatures, substrates, and water velocities. *Melanoides tuberculata* preferred cooler water, finer substrate, and slower currents than *T. clathrata*. Differences in habitat use among springsnails and *M. tuberculata* suggest that competitive interactions between these mollusks are relatively minor and that presence of the *M. tuberculata* minimally influences the abundance or habitat use of springsnails at Warm Springs.

Physiological requirements of springsnails demonstrated by Ponder et al. (1989), O'Brian and Blinn (1999), and Mlandeka and Minshall (2001) and springsnail preference for physical components of the environment at Warm Springs suggest that each taxon may be restricted to portions of a spring that provide suitable physicochemical conditions. Additionally, it suggests that springsnail abundance and distribution may be a function of factors that alter these conditions. These observations have wide implications for springsnail biogeography and conservation by suggesting that each taxon may be adapted to comparatively specific physicochemical aspects of their 'home' springs. These rather specific adaptations may be important factors limiting springsnail dispersal and restricting most taxa to springs with similar environments within a limited geographic area. Several recent articles have noted the vulnerability of springsnails to extirpation because of their limited distribution and life history requirements (e.g., Hershler, 1998; Hurt and Hedrick, 2004). Studies at Warm Springs provide quantitative evidence that springsnail abundance may be affected by any factor affecting water temperature (e.g., springbrook diversion, integrity of riparian vegetation), and the quality and heterogeneity of spring habitats. Human activities that reduce environmental heterogeneity (e.g., reduce discharge, channelize, or alter springbrook bank morphology and vegetation) are likely to reduce springsnail abundance or extirpate populations because they alter elements of the environment that define springsnail habitat. Effects of reduced habitat quality and heterogeneity by channelization, siltation, and diversion on springsnail abundance are apparent at Warm Springs where springsnails are scarce or absent from approximately 85 percent of historically occupied springbrooks. In spite of these declines, these springsnail populations appear to be comparatively resilient because their abundance rapidly increased following springbrook restoration for Moapa dace. Reestablishing springsnails in their historic range will require restoring springbrook characteristics and minimizing factors that reduce environmental heterogeneity, such as decreased discharge attributed to diversion and groundwater use.

Over the past decade, Scoppettone (1993) and Scoppettone et al. (1992) delineated characteristics of Moapa dace habitat use, and showed that adults are most common in deep, comparatively large habitats where they can hold near mid-water column and feed on drifting macroinvertebrates. This information has been integrated into conservation programs to enhance and protect Moapa dace from non-native fishes and activities that have adversely modified springbrooks and the Muddy River. Springsnail preference for relatively shallow habitats with diverse substrate composition suggests that springbrook restoration designed solely for Moapa dace may not provide sufficient heterogeneity for springsnails.

The declining status of springsnails and their sensitivity to habitat alteration is an indicator of the ecological consequences of activities that degrade springs. This suggests that changes in management are necessary to maintain biotic integrity and prevent future declines in crenobiontic species and habitats that support a large portion of the aquatic biodiversity in arid lands.

Acknowledgments. This study was funded by The Nature Conservancy, Southern Nevada Projects Office as a component of programs to conserve arid land spring systems. D. Herbst assisted with fieldwork and L. Sada assisted with laboratory identification. The manuscript was improved by comments from J. Furnish, S. Sharpe and C. Rosamond.

LITERATURE CITED

BURCH, J. B. & J. L. TOTTEHAM. 1980. North American freshwater snails. Species lists, ranges and illustrations. Walkerana 1, No. 3. 215 pp.

DE MARCO, P., JR. 1999. Invasion by the introduced aquatic snail *Melanoides tuberculata* (Müller, 1774) (Gastropoda: Prosobranchia: Thiaridae) of the Rio Doce park, Mina Gerais, Brazil. Studies on Neotropical Fauna and Environment 34:186–189.

DUDGEON, D. 1989. Ecological strategies of Hong Kong Thiaridae (Gastropoda: Prosobranchia). Malacological Review 22:39–53.

DUGGAN, I. C. 2002. First record of a wild population of the tropical snail *Melanoides tuberculata* in New Zealand natural waters. New Zealand Journal of Marine and Freshwater Research 36:825–829.

EAKIN, T. E. 1964. Ground-water appraisal of Coyote Springs and Kane Spring Valleys and Muddy River Springs area, Lincoln and Clark Counties, Nevada. State of Nevada Department of Conservation and Natural Resources, Ground-water Resources–Reconnaissance Series, Report 25.

GUTIÉRREZ, A., G. PERARA, M. YOUNG & J. A. FERNANDEZ. 1997. Relationships of the prosobranch snails *Pomacea paludosa*, *Taberia granifera*, and *Melanoides tuberculata* with the abiotic environment and freshwater snail diversity in the central region of Cuba. Malacological Review 30:39–44.

HERSHLER, R. 1994. A review of the North American freshwater snail genus *Pyrgulopsis* (Hydrobiidae). Smithsonian Contributions to Zoology Number 554.

HERSHLER, R. 1998. A systematic review of the Hydrobiid Snails (Gastropoda: Rissooidea) of the Great Basin, Western United States. Part 1. Genus *Pyrgulopsis*. The Veliger 41:1–132.

HERSHLER, R. 2001. Systematics of the North and Central American aquatic snail genus *Tryonia* (Rissooidea: Hydrobiidae). Smithsonian Contributions to Zoology, Number 612.

HERSHLER, R. & D. W. SADA. 1987. Springsnails (Gastropoda: Hydrobiidae) of Ash Meadows, Amargosa basin, California-Nevada. Proceedings of the Biological Society of Washington 100:776–843.

HILL, M. O. 1979. DECORANA—a FORTRAN program for detrended correspondence analysis and reciprocal averaging. Ecology and systematics, Cornell University. Ithaca, NY.

HUBBS, C. 1995. Springs and spring runs as unique aquatic habitats. Copeia 1995:989–991.

HURT, C. H. & P. HEDRICK. 2004. Conservation genetics in aquatic species: General approaches and case studies in fishes and springsnails of arid lands. Aquatic Sciences 66: 402–4013.

JACOBS, J. 1974. Quantitative measurement of food selection: a modification of the forage ratio and Ivlev's electivity index. Oeocologia (Berlin) 14:413–417.

JONGMAN, R. H. G., C. J. F. TER BRAAK & O. F. R. VAN TONGEREN (eds.) 1987, Data analysis in community and landscape ecology. Pudoc: Wageningen, The Netherlands.

LEVINS, R. 1968. Evolution in changing environments. Princeton University Press: Princeton, New Jersey. 120 pp.

LITTON, L. R., R. W. DAVIS & F. J. WRONA. 1981. Resource utilization indicies: an assessment. Journal of Animal Ecology 50:283–292.

MCCABE, D. J. 1998. Biological communities in springbrooks. Pp. 221–228 in L. Botosaneau (ed.), Studies in crenobiology. The biology of springs and springbrooks. Backhuys Publishers: Leiden, The Netherlands.

MLADENKA, G. C. & G. W. MINSHALL. 2001. Variation in the life history and abundance of three populations of Bruneau hot springsnails (*Pyrgulopsis bruneauensis*). Western North American Naturalist 61:204–212.

MYERS, M. J. & V. H. RESH. 1999. Spring-formed wetlands of the arid west. Islands of aquatic invertebrate biodiversity. Pp. 818–828 in D. P. Batzer, R. B. Radar & S. A. Wissiner (eds.), Invertebrates in freshwater wetlands of North America: Ecology and management. John Wiley and Sons: New York.

NOEL, M. S. 1954. Animal ecology of a New Mexico springbrook. Hydrobiologia 6:120–135.

O'BRIEN, C. D. W. & BLINN. 1999. The endemic spring snail *Pyrgulopsis montezumensis* in a high CO_2 environment: Importance of extreme chemical habitats as refugia. Freshwater Biology 42:225–234.

PALMER, M. W. 1993. Putting things in even better order: the advantages of canonical correspondence analysis. Ecology 74:2215–2230.

POLHEMUS, D. A. & J. T. POLHEMUS. 2002. Basin and ranges: The biogeography of aquatic true bugs (Insecta:Hemiptera) in the Great Basin. Pp. 235–224 in R. Hershler, D. B. Madsen & D. R. Currey (eds.), Great Basin Aquatic Systems History. Smithsonian Contributions to Earth Sciences, Number 33.

PONDER, W. F., R. HERSHLER & B. JENKINS. 1989. An endemic radiation of hydrobiid snails from artesian springs in northern south Australia: Their taxonomy, physiology, distribution, and anatomy. Malacologia 31:1–140.

PONTIER, J. P., A. THERON & G. BOREL. 1993. Ecology of the introduced snail *Melanoides tuberculata* (Gastropoda:

Thiaridae) in relation to *Biomphalaria glabrata* in the marshy forest zone of Guadeloupe, French West Indies. Journal of Molluscan Studies 59:421–428.

Richards, D. C., L. D. Cazier & G. T. Lester. 2001. Spatial distribution of three snail species, including the invader *Potamopygrus antipodarum*, in a freshwater spring. Western North American Naturalist 61:375–380.

Sada, D. W. & J. E. Deacon. 1995. Spatial and temporal variability of pupfish (genus Cyprinodon) habitat and populations at Salt Creek and Cottonball Marsh, Death Valley National Park, California. Unpublished report to the U.S. National Park Service, Death Valley, CA. 76 pp.

Sada, D. W. & G. L. Vinyard. 2002. Anthropogenic changes in historical biogeography of Great Basin aquatic biota. Pp. 277–293 in R. Hershler, D. B. Madsen & D. R. Currey (eds.), Great Basin Aquatic Systems History. Smithsonian Contributions to the Earth Sciences, Number 33.

Sada, D. W., E. Fleishman & D. D. Murphy. 2005. Associations among spring-dependent aquatic assemblages and environmental and land use gradients in a Mojave Desert mountain range. Diversity and Distributions 11: 91–99.

Sada, D. W., G. L. Vinyard & R. Hershler. 1992. Environmental characteristics of small springs in northern Nevada (abstract). Page 76 in D. A. Hendrickson (ed.), Proceedings of the Desert Fishes Council, Volume XXIII.

Schmude, K. L. 1999. Riffle beetles in the genus *Stenelmis* (Coleoptera: Elmidae) from warm springs in southern Nevada: new species, new status, and a key. Entomological News 110:1–12.

Schoener, T. W. 1970. Non-synchronous spatial overlap of lizards in patchy environments. Ecology 51:408–418.

Scoppettone, G. G. 1993. Interactions between native and nonnative fishes of the upper Muddy River, Nevada. Transactions of the American Fisheries Society 122:599–608.

Scoppettone, G. G., H. L. Burge & P. L. Tuttle. 1992. Life history, abundance and distribution of Moapa dace (*Moapa coriacea*). Great Basin Naturalist 52:216–225.

Shepard, W. D. 1993. Desert springs—both rare and endangered. Aquatic Conservation: Marine and Freshwater Ecosystems 3:351–359.

Taylor, D. W. 1985. Evolution of freshwater drainages and mollusks in western North America. Pp. 265–321 in C. J. Smiley & A. J. Leviton (eds.), Late Cenozoic history of the Pacific Northwest. American Association for the Advancement of Science: San Francisco.

ter Braak C. J. F. & I. C. Prentice. 1988. A theory of gradient analysis. Adv. Ecol. Res. 18:271–313.

U.S. Fish and Wildlife Service. 1996. Recovery plan for the rare aquatic species of the Muddy River ecosystem. U.S. Fish and Wildlife Service: Portland, Oregon.